Comments on the sternal morphology of Australasian pigeons

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In most avian families, the morphology of the sternum is markedly uniform. A striking exception is the range of conditions exhibited among the pigeons (Columbidae), particularly in the shape and size of the incisurae, trabeculae and corpus sterni. Because these various structural states show a strong correspondence with certain postulated subgroups in the pigeons, their distribution can be a useful systematic tool. The greatest range of sternal morphology occurs among the species of Australasia (Australia, New Guinea, New Zealand and New Caledonia). The relationships of some of the lesser known forms and the generic limits in some of the Australian species have been unresolved. Most of these have one of the distinctive sternal morphologies characterizing the various subgroups.

As part of their description of the Rodriguez Solitaire *Pezophaps solitaria,* Newton & Newton (1869) briefly discussed the variation in sternal morphology in the Columbidae and illustrated several of the states found in Australasian genera. Shufeldt (1901) made passing reference to the variation found by Newton & Newton (1869), but largely restricted his description of the pigeon sternum to the states exhibited by North American taxa. In his examination of the osteology of the Columbiformes, Martin (1904) discussed a number of characters of the sternum, but devoted few comments to the variation and distribution of the incisurae and trabeculae within the order, and in his proposed systematic arrangement of the pigeons afforded little weight to the configuration of these features. Verheyen (1957) noted the variation in this family, recognizing six main types, which he incorporated into his revision of the pigeons; however, the taxa he sampled omitted a number of important Australasian forms. The condition of the sternum is reported on here for all Australasian genera of pigeons, represented by at least one species each, which are given in Appendix 1. Osteological terminology follows Baumel & Witmer (1993), except that as terms of position and direction anterior is used rather than rostral and posterior rather than caudal.

The variation in morphology of concern here is in the position, size and extent of the incisurae and trabeculae of the margo costalis and caudalis. The incisura medialis may be notched (open posteriorly) or perforated (enclosed posteriorly by a bony border=fenestra medialis). Within some taxa, the incisura medialis is subject to intraspecific variation, and occasionally both conditions may occur in the same individual. In other genera, only one state is evident.

The sternal morphology that characterizes the 'typical', unspecialized forms, such as *Columba, Zenaida* and *Streptopelia,* is found uniformly in North American (Shufeldt 1891) and European genera.

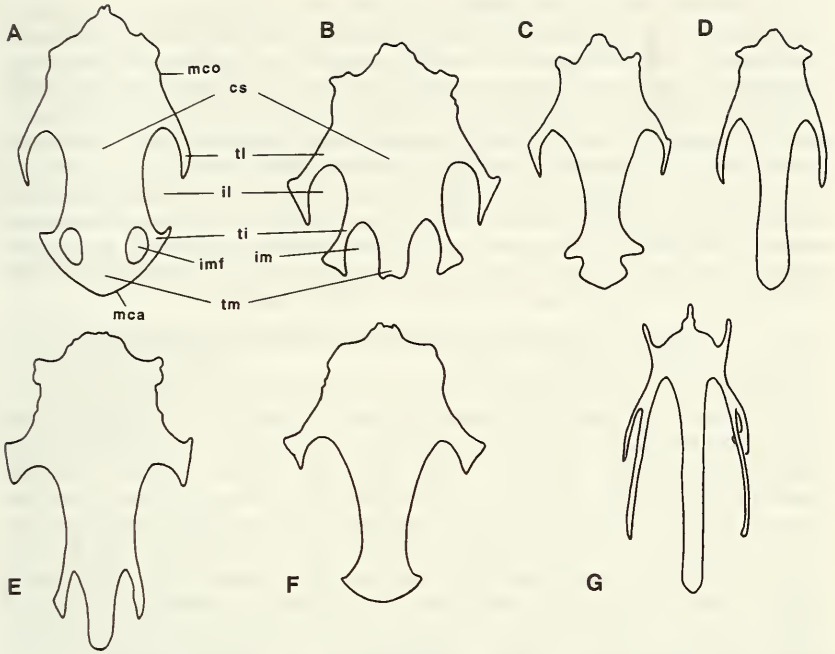

Figure 1. Outlines of the sterna of selected Australasian pigeons, showing the range of morphological variation in the incisurae, trabeculae and corpus sterni, with the sternum of a partridge for comparison: (a) *Columba livia;* (b) *Ptilinopus magnificus;* (c) *Ocyphaps lophotes;* (d) *Petrophassa smithii;* (e) *Goura cristata;* (f) *Didunculus strigirostris;* (g) *Perdix perdix*. Sterna (a–d) and (f) shown to the same scale, (e) reduced by about half relative to these, and (g) reduced to approximate (d) in size. Abbreviations: **cs,** corpus sterni, **il,** incisura lateralis, **im,** incisura medialis, **ifm,** incisura (fenestra) medialis, **mca,** margo caudalis, **mco,** margo costalis, **ti,** trabecula intermedia, **tl,** trabecula lateralis, **tm,** trabecula mediana.

Differences between this and other sternal morphologies represent either reduction in size or hypertrophy of these features, or by a shift in their positions.

Group 1: Columba, Streptopelia, Macropygia, Reinwardtoena, Phaps

In the typical columbid sternum (Fig. 1a; also see Newton & Newton 1869, Plate XXXIII, Fig. 169; Martin 1904, Fig. O^3a), the trabecula lateralis joins the margo costalis about a third of the way from the anterior end. The trabecula lateralis is usually broad and straight for most of its length, although the posterior margin is concave. The lateral end curves posteriorly into a distinct point to about the sternal midpoint. The trabecula intermedia is broad, but shorter than the trabecula lateralis. The end is expanded both anteriorly and posteriorly, a condition termed herein as "booted". This boot is pointed anteriorly, while its posterior portion usually connects with the trabecula mediana,

closing off the incisura medialis into a fenestra. The incisura lateralis is long (about a third of the length of the sternum); its width is about a third to a half of its length. Its medial margin is concave, which in some specimens makes the corpus sterni relatively thinner, producing a waisted appearance. The fenestra (incisura) medialis is about a third or less the size of the incisura lateralis, and almost always enclosed posteriorly. The trabecula mediana is broad, and the margo caudalis is rounded or has a posteriorly-directed rounded point. *Phaps* differs by having the posterior end somewhat narrower in *P. chalcoptera* and, most noticeably, *P. elegans*; in *P. histrionica*, however, it is not markedly different from that of the other genera. The sternum of *Phaps chalcoptera* was illustrated by Martin (1904, Fig. P^3a).

Group 2: Ptilinopus, Ducula, Lopholaimus, Gymnophaps, Drepanoptila, Hemiphaga, Treron, Alectroenas

Another condition (Fig. 1b; also see Martin 1904, Figs. S^3a, T^3a, U^3a) differs from that in *Columba* by having the lateral margin of the trabecula lateralis booted, extending into both anteriorly- and posteriorly-directed points. The posterior point often extends posteriorly beyond the sternal midpoint. The trabecula intermedia is proportionally longer than in the typical condition. The end is booted, but the posterior margin joins the trabecula mediana less often. The margin of the incisura lateralis between the bases of the trabeculae lateralis and intermedia is straight or only slightly waisted, and corpus sterni is proportionally wider. The incisura medialis is larger relative to the incisura lateralis, in part because of the greater length of the trabecula intermedia. In most specimens, the incisura medialis is not enclosed posteriorly, although in individuals one or both may be fenestra. The margo caudalis is straight or slightly indented at its midpoint.

Other conditions of the sternum

Different changes are exhibited by the other Australasian genera. There is a progressive narrowing of the corpus sterni posterior to the trabecula lateralis and a reduction in the trabecula intermedia and the incisura medialis. Among these genera, the trabecula lateralis exhibits opposite trends, in most taxa becoming increasingly gracile, but in two becoming more robust.

Group 3: Ocyphaps

Ocyphaps (Fig. 1c) resembles *Phaps* in the anterior portion of the sternum except that the trabecula lateralis originates more anteriorly and by being narrower throughout, without the degree of anterior divergence of the lateral borders. Differences that are more substantial occur in the posterior end. The trabeculae intermedia and mediana are short (15% of length), the former having little terminal lateromedial expansion, the incisura medialis is short and more circular, and the margo caudalis is straighter.

Other pigeon genera

Chalcophaps, Henicophaps, Gallicolumba, Geopelia, Leucosarcia, Trugon, Geophaps and *Petrophassa* have the trabecula lateralis much

thinner and curved over its entire length. The lateral end curves posteriorly to about the sternal midpoint, terminating in a distinct point, short posterior projection or very small boot (expanded anteriorly and posteriorly). Most of these genera resemble *Ocyphaps* in the tendency towards substantial narrowing and reduction of the features of the posterior end, although the extent of reduction varies. There are also differences in the degree of lateral divergence of the anterior end. A consequence of the respective anterior and posterior repositioning of the trabeculae lateralis intermedia is that the incisura lateralis is much longer (up to 50% of sternal length) and the incisura medialis shorter.

Group 4: Leucosarcia, Chalcophaps, Henicophaps, Geopelia, Gallicolumba, Trugon

Leucosarcia shows only minor reduction, limited mainly to an overall narrowing of the posterior end. The trabeculae and incisura are moderately long and the margo caudalis somewhat pointed. The anterior end is moderately narrow, and the trabecula lateralis extends posteriorly past the midpoint of the sternum (see Newton & Newton 1869, Plate XXXIII, Fig. 171). Limited reduction is also evident in *Chalcophaps, Henicophaps* and *Geopelia* (for *Geopelia,* see Newton & Newton 1869, Plate XXXIII, Fig. 175). These are similar to *Leucosarcia,* with some intrageneric variation in the relative lengths of the posterior features and roundedness of the margo caudalis. *Chalcophaps* is proportionally broader at the anterior end. The trend in reduction is continued in *Gallicolumba* and *Trugon.* A specimen of *G. luzonica* is noticeably narrower than one of *G. jobiensis.* As in *Trugon,* the sternum in this species is narrower over the entire length.

Group 5: Geophaps, Petrophassa

The greatest expression of reduction of the sternum occurs in *Geophaps* and *Petrophassa* (Fig. 1d), in which the trabecula intermedia is absent. Because of this, the incisura lateralis is unbounded distally; its width is greater than the corpus sterni and about two-thirds its length. Likewise, there is no distinct incisura medialis. The lateral margins of the corpus sterni are concave, which is thus slightly waisted in the middle before curving laterally into the trabecula mediana. The corpus sterni is narrow over its entire length, particularly distal to the junction with the trabecula lateralis. The trabecula mediana is narrow, and the margo caudalis is rounded.

Group 6: Goura, Caloenas

An opposite trend in the development of the trabecula lateralis occurs in *Goura* and *Caloenas* (Fig. 1e; also see Newton & Newton 1869, Plate XXXIII, Fig. 176, and Martin 1904, Fig. R^3 for *Goura*). In these genera, the trabecula lateralis is broad (markedly so in *Goura*), which is a result of both anterior and posterior expansion. The trabecula is directed more laterally, and the end extends posteriorly in a

large triangular projection (to or beyond anteroposterior midpoint of the sternum). These taxa differ in the configuration of the posterior section. In *Goura* the incisura medialis are relatively long and elliptical, and the trabecula intermedia slender and moderately long (originating about 20% of the way from the posterior end), whereas in *Caloenas* all are shorter (the trabecula intermedia originates nearer the posterior end and is about 15% of sternal length) and the trabeculae intermedia are proportionally broad with slight terminal boots.

Group 7: Didunculus

Didunculus (Fig. 1f; Newton & Newton 1869, Plate XXXIII, Fig. 170; Martin 1904, Fig. V^3a) shows an unusual combination of features. The trabecula lateralis originates about a quarter of the way from the anterior end, and is short, broad throughout its length and somewhat concave on the posterior margin; it terminates in a short posterior projection, and resembles *Caloenas* in being directed more laterally than in most genera. The trabecula intermedia and the incisura medialis are absent. The posterior half of the corpus sterni is narrow and waisted, before flaring laterally on the trabecula mediana. The margo caudalis is straight.

Systematic aspects

Verheyen (1957) divided the morphological states of the pigeon sternum into six major types. The first was that characteristic of *Columba,* variations of which occurred in *Streptopelia* and *Macropygia.* The second was characterized as the *Oena*-type, which was also found in *Phaps*. There were several variations of this state, including one seen in *Goura,* another in *Didunculus* and a third in *Ducula, Ptilinopus* and *Treron.* The *Geopelia*-type also included *Leucosarcia* and *Ocyphaps,* with different variations exhibited by *Chalcophaps* and *Otidiphaps*. The fourth type was restricted to *Gallicolumba,* the fifth included *Geophaps* and *Megaloprepia* (=*Ptilinopus magnificus*), and the last only *Starnoenas,* a New World genus.

Some of these groupings are similar to those described in this paper, but others are quite divergent. The most striking anomaly is the association of *Geophaps* with *Ptilinopus magnificus*. The inclusion of the other fruit pigeons with *Goura* and *Didunculus* is also at considerable variance with the results of this work. Verheyen (1957) used taxa from a much wider geographic area (i.e. the world) than just Australasia, but this should not have affected the conclusions in this manner.

The morphology of the sternum is not sufficient in itself to be the sole criterion on which to base taxonomic decisions. Nonetheless, it is a useful adjunct to other characters in establishing relationships in the Columbiformes. In some instances, where there is a dichotomy of opinion, this character can provide strong support for one proposal.

The fruit pigeons (Treroninae) have their centre of diversity in Australo-Papua, where *Ptilinopus* and *Ducula* dominate, extending east to islands of the Pacific Ocean, west into Indonesia and north to the Philippine Islands, with outliers in Africa and Southeast Asia (*Treron, Alectroenas*). There are several monotypic genera in Australasia. The

sternal morphology is uniform among the genera. The placement of most of the genera has been relatively consistent among authors, although two genera have been placed elsewhere in the family by some authors. *Gymnophaps* of New Guinea and the Solomon Islands was placed in *Columba* by Salvadori (1893), and kept separate but adjacent to *Columba* in the subfamily Columbinae by Peters (1937); Goodwin (1970) believed its affinities were with the fruit pigeons. The morphology of the sternum is that of a fruit pigeon, and supports Goodwin's action.

The phabine pigeons of Australo-Papua are of special interest. There has been considerable disagreement about the limits of the nominal genera *Phaps, Ocyphaps, Henicophaps, Geophaps, Petrophassa, Histriophaps* and *Lophophaps*. Goodwin (1970), followed by Condon (1975), merged *Histriophaps* with *Phaps,* an action now accepted by most authors, and *Lophophaps* and *Geophaps* with *Petrophassa*. Frith (1982) and Christidis & Boles (1994) maintained *Geophaps,* including *Lophophaps,* distinct from *Petrophassa*. Schodde (1982) synonymized *Ocyphaps* with *Petrophassa*. The placement of *Histriophaps* with *Phaps* is supported by sternal morphology. The unusual and highly derived morphology found in *Petrophassa* and *Geophaps* argues that they are certainly sister-taxa, and the decision to consider them congeneric may be justified. Conversely, the merger of *Ocyphaps* with *Petrophassa-Geophaps* is not supported by sternal morphology. This former genus is somewhat intermediate between these genera and *Phaps* in its degree of reduction of the trabecula mediana and the incisura medialis, but overall shows a greater resemblance to the latter. The intermediate morphology is not surprising given the current recognition of *Ocyphaps* as a monotypic genus, placed between these groups in a linear sequence (e.g. Christidis & Boles 1994). Further evidence is required before the closest relatives of *Ocyphaps* in the phabine assemblage can be decided.

Frith (1982) was among the authors that have remarked on the structural and behavioural convergence by species of *Petrophassa-Geophaps* on partridges and similar-sized gallinaceous birds, which are absent in Australia. The similarities extend to the sternal morphology. Partridges, like *Petrophassa-Geophaps,* have a very long slender trabecula lateralis, which is situated far anteriorly, and a narrow corpus sterni and trabecula mediana, bordered by a very long incisura (Fig. 1g). Whether this convergence in morphology of the sternum reflects mechanical convergence between these taxa in the action of the pectoral and supracoracoideus muscles invites investigation. These pigeons, like similarly sized partridges, have a markedly rapid take off.

Leucosarcia, Chalcophaps, Henicophaps, Trugon and *Geopelia* share roughly similar sternal morphologies characterized by varying degrees of reduction. These resemblances may not be due to close relationships among these genera, and the diversity of body form and behaviour argues against these forming a monophyletic assemblage. The sterna may only demonstrate a superficially similar stage of initial divergence from the typical columbid morphology.

Goura and *Caloenas* have been grouped either implicitly in a linear sequence, usually near the start, or explicitly in their own subgroup

within the family. The sternal morphologies of these taxa differ from the typical condition in the same manner. The trends in their variation are unlike those observed in other divergent groups of Australo-Papuan pigeons, and suggest that these features are valid indicators of relationship.

The monotypic *Didunculus* of Samoa exhibits a unique suite of sternal characters. This taxon has uncertain affinities, and the unusual sternal morphology reflects this. It has been suggested that *Didunculus* represents a somewhat transitional form between pigeons and parrots. The psittaciform sternum is similar in some respects to the morphology of *Columba* in the shape of the corpus sterni and position of the incisura medialis. The sternum of *Didunculus* shows little resemblance to that of either parrots or typical pigeons, and thus seems unlikely to represent the morphology expected in a mutual ancestor of these orders.

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Appendix

Species of pigeons for which the sternum was examined. *Caloenas nicobarica; Chalcophaps indica; Columba: leucomela, livia, vitiensis; Didunculus strigirostris; Drepanoptila holosericea; Ducula: bicolor, concinna, mullerii, whartoni; Gallicolumba: jobiensis, luzonica; Geopelia: cuneata, humeralis, striata; Geophaps: plumifera, scripta, smithii; Goura cristata; Gymnophaps albertisii; Hemiphaga novaeseelandiae; Henicophaps albifrons; Leucosarcia melanoleuca; Lopholaimus antarcticus; Macropygia amboinensis; Ocyphaps lophotes; Otidiphaps nobilis; Petrophassa: albipennis, rufipennis; Phaps: chalcoptera, elegans, histrionica; Ptilinopus: magnificus, regina, rivoli, superbus; Reinwardtoena reinwardtsi; Streptopelia: chinenis, risoria; Treron psittacea; Trugon terrestris; Zenaida auriculata.*

A reassessment of the subspecies in the owl *Glaucidium tephronotum*, with notes on its biology

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The Red-chested Owlet *Glaucidium tephronotum* is a relatively little-known Afrotropical forest resident. Six subspecies, *tephronotum*, *pycrafti*, *medje*, *elgonense*, *lukolelae* and *kivuense*, have been described, of which only the first four have been retained by *The Birds of Africa* (Fry *et al.* 1988; hereafter referred to as *BoA*). After careful examination of 46 specimens, representing all known taxa (see Table 1), we have come to the conclusion that only the first three subspecies should be recognised.

This study became necessary because PH was confronted with the substantial differences in measurements and weights that exist between birds of West Africa and those of the Democratic Republic of Congo (Central Africa) and eastern Africa as published by several authors, here grouped in Table 2. Chapin (1932), Bannerman (1933, 1951) and Prigogine (1971) previously pointed out these differences. However, the treatment in *BoA* and the measurements given appear to be incomplete and partly inaccurate. One may further wonder why in this reference work the juvenile and immature remain undescribed, notwithstanding the presence of a young bird in the collections of the Koninklijk Museum voor Midden-Afrika, Tervuren (KMMA), which was indicated previously by Chapin (1939).